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## Temporal variability of a single population can determine the vulnerability of communities to perturbations

Mrowicki, R. J., O'Connor, N. E., & Donohue, I. (2016). Temporal variability of a single population can determine the vulnerability of communities to perturbations. *Journal of Ecology*, 104(3), 887-897.  
<https://doi.org/10.1111/1365-2745.12533>

**Published in:**  
Journal of Ecology

**Document Version:**  
Peer reviewed version

**Queen's University Belfast - Research Portal:**  
[Link to publication record in Queen's University Belfast Research Portal](#)

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1       **TEMPORAL VARIABILITY OF A SINGLE POPULATION**  
2       **CAN DETERMINE THE VULNERABILITY OF**  
3       **COMMUNITIES TO PERTURBATIONS**

4  
5       ROBERT J. MROWICKI<sup>\*1</sup>, NESSA E. O'CONNOR<sup>1</sup> AND IAN DONOHUE<sup>2,3</sup>

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10   **Running head:** Population variability and perturbations  
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13  
14   **Type of article:** Standard paper  
15

16   **Word count:** 325 (summary); 8,696 (main text, references, tables and figure captions)

## Summary

1. Many aspects of global change affect the variability of species population densities, in terms of both the magnitude and pattern of density fluctuations. However, we have limited empirical understanding of the consequences of altered temporal variability of populations, independent of changes in their mean densities, for the structure and stability of natural communities and the responses of ecosystems to additional stressors.
2. We used a field experiment to test the effects of altered temporal variability of a single consumer species on community structure and stability. Specifically, we manipulated the temporal variability of populations of a key grazer species on temperate rocky shores (*Littorina littorea*), independent of their mean densities, over 12 months and measured the responses of algal communities in terms of multiple measures of structure and stability. Further, we tested whether consumer variability determined the effects of an additional perturbation, elevated sedimentation, on algal communities.
3. The effects of sedimentation on the structure and stability of algal communities were regulated by the temporal variability of consumer populations. In particular, elevated sedimentation led to a decrease in algal evenness, but only when consumer densities were held constant, and resulted in a decrease in the rate of local algal extinctions, but only when consumer temporal variability was increased.
4. Independent of sedimentation, increased temporal variability of consumer populations led to a shift in algal assemblage structure and affected the stability of algal communities in terms of both compositional turnover and resistance to environmental perturbations. Further, these effects varied according to the temporal pattern of consumer density fluctuations.

41 5. *Synthesis*. Our results demonstrate that changes in the temporal variability of a single  
42 species can modify multiple aspects of both the structure and stability of natural  
43 communities and alter their responses to perturbations. **However**, the effects of consumer  
44 variability cannot be predicted without knowledge of the temporal pattern of density  
45 fluctuations. These findings have profound implications for our understanding of the  
46 effects of multiple disturbances on ecosystems.

47  
48 **Key-words:** algae, diversity, ecosystem functioning, field experiment, *Littorina littorea*,  
49 multiple stressors, plant–herbivore interactions, rocky intertidal, sedimentation, stability

## Introduction

Human-induced global environmental change is threatening the functioning and stability of Earth's ecosystems and the valuable services **that** they provide (Vitousek *et al.* 1997; Millennium Ecosystem Assessment 2005; Cardinale *et al.* 2012; Hooper *et al.* 2012). **In addition to the intensification of multiple environmental stressors (IPCC 2014),** many aspects of global change are expected to alter the frequency, variance and timing of disturbances (Easterling *et al.* 2000; **Rhein *et al.* 2013**), the **complex ecological** consequences of which may be difficult to predict (Benedetti-Cecchi *et al.* 2006; García Molinos & Donohue 2010, 2011; Pincebourde *et al.* 2012). **In light of these concerns, there has been increasing emphasis on the importance of spatial and temporal variability, versus the mean intensity, of ecological processes and their environmental drivers (Benedetti-Cecchi 2003; Bertocci *et al.* 2005; Atalah, Anderson & Costello 2007; Stier *et al.* 2013).**

**Densities of consumers and the strengths of their interactions with prey are naturally heterogeneous in both space and time, as a result of intrinsic community dynamics and exogenous environmental forcing (Butler 1989; Navarrete 1996; Berlow 1999; Lauzon-Guay & Scheibling 2009). The variability of specific consumer populations may also be modified by human activities (Adler, Raff & Lauenroth 2001; Castilla & Defeo 2001). Several common ecosystem management practices, such as those in agricultural systems, in fisheries and in many forms of conservation, are based on the direct manipulation of the biomass of one, or perhaps a few, focal species, altering the temporal variability of their population densities in different ways. For example, the harvesting of commercial wild species in marine systems often follows 'boom and bust' trends, increasing the variability in biomass of key consumers (Castilla & Defeo 2001; Worm *et al.* 2006), while management of livestock tends to promote**

the reduction of grazing variability in terrestrial systems (Adler, Raff & Lauenroth 2001). Within communities that are regulated largely by interactions between herbivores and primary producers, such as in marine benthic habitats and various kinds of agricultural systems (Hawkins & Hartnoll 1983; Shurin *et al.* 2002), changes in grazing variability may have profound consequences for ecosystem structure, functioning and stability (Benedetti-Cecchi *et al.* 2005; Atalah, Anderson & Costello 2007).

The importance of structural properties of communities in regulating their stability has comprised a key focus of both theoretical and empirical research in ecology for decades (e.g. MacArthur 1955; May 1972; Montoya, Pimm & Solé 2006; Allesina & Tang 2012). However, our understanding of the reciprocal relationship between community structure and stability remains limited (Rooney & McCann 2012). This is, in part, because ecological stability is a multidimensional concept, incorporating components such as spatial and temporal variability, resistance, resilience, robustness and persistence (Table 1; Pimm 1984; Ives & Carpenter 2007), but the vast majority of research has focussed on single components in isolation. Recent experimental research (Donohue *et al.* 2013) has demonstrated that different components of stability can be strongly related to each other, but also that the strength and nature of relationships among them may be disrupted when communities are exposed to strong perturbations. Therefore, simultaneous quantification of multiple components of stability is needed to provide comprehensive understanding of how communities may be destabilised by structural change and perturbations (Donohue *et al.* 2013). Theory suggests that changes in the population dynamics of key components of food webs could have considerable knock-on consequences for the stability of whole ecosystems (Pimm 1982; Rooney & McCann 2012). Further, empirical research has demonstrated how variability in consumer–resource interactions can promote spatial variability in marine

intertidal communities (Berlow 1999; Benedetti-Cecchi 2000; Benedetti-Cecchi *et al.* 2005). Consumer variability may also affect other components of stability, such as temporal variability, indirectly via shifts in assemblage structure or diversity (Jiang & Pu 2009; Rooney & McCann 2012). Currently, however, we have little empirical understanding of the consequences of alterations to the variability of consumer populations, independent of changes in their mean densities, for the multidimensional stability of natural communities.

Here, we examine how altering the temporal variability of populations of a key consumer species, independent of changes in their mean densities, affects the structure and multiple components of the stability of communities in a natural ecosystem. Specifically, we manipulated the temporal variability of a key grazer, the periwinkle *Littorina littorea*, experimentally in natural rocky intertidal communities and examined the responses of both microalgal and macroalgal assemblages to subsequent perturbation in the form of sedimentation. *Littorina littorea* plays a significant role in the dynamics of benthic communities in the north Atlantic (Bertness 1984; Jenkins *et al.* 2008; O'Connor *et al.* 2015) and is subjected to unregulated harvesting in many areas (McKay & Fowler 1997; Cummins *et al.* 2002). This can promote high population variability over small spatial and temporal scales in intertidal habitats (Johnson *et al.* 2008). In addition to anthropogenic impacts on the abundance and variability of key consumer species, coastal habitats are also subjected to a variety of interacting abiotic pressures at local and global scales (Thompson, Crowe & Hawkins 2002; Halpern *et al.* 2008). Sedimentation, arising from both natural and anthropogenic processes, is a particularly widespread and pervasive form of disturbance that has profound consequences for the structure and dynamics of coastal marine ecosystems, including rocky shores (Airoldi 2003). Further, as a result of human activities that enhance riverine inputs and exacerbate coastal erosion, sediment loading in coastal areas is expected to

increase over the coming decades throughout the globe (Thompson, Crowe & Hawkins 2002). Despite the potential for such abiotic stressors to interact with important consumer-driven processes (Bertness 1984; Airolidi & Hawkins 2007; O'Connor & Donohue 2013; Mrowicki & O'Connor 2015), it is not yet known how altered patterns of consumer variability modify the responses of natural communities to perturbations.

Based on previous empirical research examining the responses of assemblages to increased temporal variability of consumers in aquatic systems (e.g. Butler 1989; Navarrete 1996; Atalah, Anderson & Costello 2007), we hypothesised that changing the temporal variability of *L. littorea* populations, independent of their mean densities, would alter the biomass and structure of natural algal assemblages. Additionally, we expected that increased consumer population variability would destabilise algal assemblages in terms of multiple components of their stability, either directly or indirectly via changes in community structure, as well as determine their responses to perturbation in the form of elevated sedimentation. Given that the dynamics of marine communities often depend strongly on the timing of consumer and environmental variability (Bertocci *et al.* 2005; Stier *et al.* 2013), we also explored whether the effects of changes in consumer variability were regulated by the timing of fluctuations in population density.

## Materials and Methods

### *Experimental site*

The experiment was conducted on a moderately exposed rocky shore at Rush, Co. Dublin, on the east coast of Ireland (53.524°N, 6.078°W). The shore comprised a mosaic of patches of



bare emergent substratum, barnacles (predominantly *Austrominius modestus* and *Semibalanus balanoides*) and mussels (predominantly *Mytilus edulis*). Macroalgal assemblages consisted mostly of red algal turfs (*Mastocarpus stellatus*, *Osmundea* spp. and *Gracilaria gracilis*) interspersed with green filamentous species (*Cladophora rupestris*, *Ulva* spp. and *Chaetomorpha linum*), overlain by sparse canopies of brown macrophytic algae (*Fucus vesiculosus*). Encrusting macroalgae (*Lithothamnion* spp. and *Ralfsia verrucosa*) were common on bare rock and barnacles. By far the most abundant gastropod grazer on the shore was the common periwinkle, *Littorina littorea* (hereafter '*Littorina*'; density  $300.8 \pm 24.5 \text{ m}^{-2}$  [mean  $\pm$  SE;  $n = 16$ ]). Other grazers were present at much lower densities, including the topshell *Gibbula umbilicalis* ( $36.8 \pm 7.3 \text{ m}^{-2}$ ), the limpet *Patella vulgata* ( $16.0 \pm 3.7 \text{ m}^{-2}$ ) and other littorinids, such as *L. saxatilis* and *L. obtusata*.

### *Experimental design*

We established 40 experimental plots ( $35 \times 35 \text{ cm}$ ) within mussel beds around mid-tidal level (ca. 2.0 m above Chart Datum). To enable the manipulation of consumer densities, plots were enclosed by 12 cm-high cages, consisting of square fences with attached lids, constructed from stainless steel mesh (0.9 mm wire diameter, 4.17 mm aperture, 67% open area) fixed to the substratum with screws and washers. The cages were used to restrict the movement of adult *Littorina* while allowing exposure to natural environmental dynamics and access to smaller mobile consumers, including annelid and nemertean worms, amphipods and juvenile gastropod grazers, in addition to propagules of sessile benthic fauna and algae. One month prior to the commencement of the experiment, mussels and associated sediment, fauna and algae were transplanted into cages from an adjacent area on the shore to ensure that the initial

cover of mussels within cages ( $61.4 \pm 1.0\%$  [mean  $\pm$  SE]) was similar in all treatments and representative of background abundances on the shore (O'Connor *et al.* 2013).

To increase the applicability of our findings to real-world ecosystems, we established an additional eight uncaged manipulated plots, which enabled the comparison of consumer variability and algal assemblage dynamics in our caged plots with natural patterns on the shore. The uncaged plots were interspersed haphazardly among the caged plots and contained similar cover of mussels (range 53–78%). The uncaged plots were, however, not used as true procedural controls for detecting cage artefacts because it was not possible to manipulate, *a priori*, consumer variability within caged plots independent of the mean density to reflect robustly the natural spatiotemporal dynamics at similar spatial scales on open areas of the shore. Nonetheless, we opted to conduct our experiment on open natural communities in the field because field experiments have a distinct advantage over laboratory- or mesocosm-based studies with regards to the incorporation of natural environmental heterogeneity and enhanced realism (Naeem 2008). Further, numerous studies conducted on this shore and elsewhere using an identical cage design have demonstrated an absence of cage effects on the structure and stability of algal assemblages over similar or longer timescales (e.g. O'Connor & Crowe 2005; O'Connor *et al.* 2011, 2013; Donohue *et al.* 2013).

Three experimental treatments were established in August 2012 to test the effects of consumer variability on algal assemblages over 12 months. Importantly, the mean density of *Littorina* was identical in all of our experimental plots (both caged and uncaged) over the duration of the experiment, mimicking the mean background density on the shore (Fig. 1a,b), and was unconfounded from the manipulation of consumer variability (Fig. 1c). In the 'constant' treatment, *Littorina* density was maintained at 30 individuals per plot for the

duration of the experiment to mimic situations where the density of consumers is relatively constant over time. We established two ‘variable’ treatments to test the importance of the temporal pattern of consumer density fluctuations. *Littorina* density in both of these treatments alternated between 15 and 45 individuals per plot every two months (Fig. 1a). This was within the range of background densities observed in preliminary surveys at the experimental site (128–464 m<sup>-2</sup>). The ‘variable<sub>1</sub>’ treatment commenced with 15 *Littorina* individuals per plot, while the ‘variable<sub>2</sub>’ treatment commenced with 45 (Fig. 1a). All experimental densities were based on adult individuals (> 5 mm) because it was impractical to manipulate juveniles smaller than the cage mesh size. The mean density of juvenile *Littorina* was quantified over the duration of the experiment and did not vary among our caged biotic variability treatments (ANOVA; MS = 0.44,  $F_{2,17} = 0.39$ ,  $P = 0.681$ ).

To test whether variability in consumer population densities altered the responses of communities to disturbances, we established two sedimentation treatments (‘ambient’ and ‘elevated’) four months after the commencement of the experiment. The elevated sedimentation treatment involved the monthly addition of 400 g dry mass of sandy sediment, collected from an adjacent sandy shore, to each respective plot until the end of the experiment (12 months). This sedimentation rate, equivalent to ca. 100 g m<sup>-2</sup> d<sup>-1</sup>, is within the range experienced by coastal habitats in the vicinity of populated areas (Airoidi & Virgilio 1998; Connell 2005). **Instead of a temporally consistent increase in sedimentation above background levels, which would have been impossible to maintain for the duration of the experiment, this treatment was manifested as a pulse disturbance, whereby the full quantity of sediment was applied to each respective plot at low tide and then apparently washed away by the incoming tide.** The two sedimentation treatments were crossed fully with the three biotic variability treatments, yielding a total of six treatments in a factorial design. Eight replicate

caged plots were assigned randomly to each of the four treatment combinations involving the constant and variable<sub>1</sub> consumer variability treatments. However, owing to practical limitations on the number of plots that could be maintained during the experiment, it was not possible to allocate such a large number of replicates to all treatments. Consequently, four replicate caged plots were assigned randomly to the remaining two treatment combinations involving the variable<sub>2</sub> treatment.

The percent cover of macroalgal species was estimated monthly using a 25 × 25 cm quadrat with 64 intersections, positioned centrally within cages to avoid sampling edge effects. Species present within the quadrat but not occurring underneath any of the intersections were assigned a value of 1% (O'Connor & Crowe 2005). Slate tiles (10 × 10 × 1 cm) were either attached inside cages or fixed to the substratum adjacent to uncaged plots four months after the commencement of the experiment to monitor the development of epilithic biofilms. Microalgal biomass on the tiles was quantified monthly *in situ* by measuring chlorophyll *a* concentrations with a benthic fluorometer (BenthosTorch, bbe Moldaenke GmbH, Schwentinental, Germany). This method has been shown to provide reliable estimates of total microalgal biomass in marine intertidal systems (Kahlert & McKie 2014), and enables the differentiation of component microalgal groups (diatoms, cyanobacteria and chlorophytes) based on their fluorescence excitation spectra (Aberle *et al.* 2006). Mean values for each plot were calculated from three haphazardly-spaced readings per tile because the distribution of epilithic microalgae is highly heterogeneous at small scales (Hutchinson *et al.* 2006). Quantification of all response variables commenced four months after the establishment of the experiment (i.e. from December 2012 to August 2013) to avoid transient dynamics (Donohue *et al.* 2013).

## Data analyses

Given the dynamic nature of algal communities on rocky shores and their rapid responses to fluctuations in physical and biological conditions at scales relevant to this study (e.g. Hawkins & Hartnoll 1983), focussing on primary producer assemblages allowed us to maximise the probability of detecting shifts in ecosystem functioning and stability (Borrvall & Ebenman 2006; Donohue *et al.* 2013). Therefore, we used the total biomass of microalgae and the total cover, taxonomic richness, Simpson's evenness ( $1-\lambda$ ) and assemblage structure of macroalgae at the end of the experiment as proxies for shifts in ecosystem functioning. There were no significant differences in any of these variables among treatment combinations (including between caged and uncaged plots) at the start of the experiment (Table S1 in Supporting Information).

We quantified up to six components of ecological stability for algal assemblages (Table 1): spatial and temporal variability of total biomass were calculated for both micro- and macroalgal assemblages, while the number of local species extinctions and invasions, compositional turnover and resistance to environmental fluctuations were determined for macroalgal assemblages only, owing to low taxonomic resolution of the microalgal data. Both spatial and temporal variability were detrended to avoid the potentially confounding effects of transient or seasonal shifts in algal abundance over the duration of the experiment. This was achieved by using the residuals from linear regressions of total algal abundance (microalgal biomass or macroalgal cover) against time, rather than algal abundance *per se* (Tilman, Reich & Knops 2006; Donohue *et al.* 2013).

We tested for effects of the nature and timing of variability in consumer densities and for interactions between these and sedimentation on measures of each of the structure, functioning and stability of algal communities. Our statistical models incorporated two fully-crossed factors, consumer variability (fixed, three levels: constant, variable<sub>1</sub> and variable<sub>2</sub>) and sedimentation (fixed, two levels: ambient and elevated). In the case of spatial variability, for which data were not associated with individual plots, month was included as a random factor in all analyses to account for variation among survey dates.

Permutational analysis of variance (perANOVA; Anderson 2001a), based on Euclidean distance matrices, was used to test hypotheses involving univariate metrics of ecosystem functioning and stability. Homogeneity of data was assessed prior to analysis using Levene's test and data were transformed as necessary to stabilise heterogeneous variances. We used permutational procedures rather than conventional ANOVA in our analyses because they do not rely on the normality of error distributions, an assumption to which univariate ecological data often do not conform (Anderson 2001a), and because these methods have been shown to be significantly more robust for the analysis of unbalanced datasets than other resemblance-based permutation methods (Anderson & Walsh 2013). We tested the consistency of the perANOVA results by comparing pseudo-*F* values obtained for all terms against distributions of *F*-values obtained from conventional ANOVAs performed on 10<sup>4</sup> balanced datasets (*n* = 4) sampled randomly from the full dataset. All relevant test statistics were within the 95% confidence intervals derived from this procedure (Table 2).

We tested for differences in the structure of macroalgal assemblages using permutational multivariate analysis of variance (PERMANOVA; McArdle & Anderson 2001; Anderson 2001b) based on Bray-Curtis dissimilarities and calculated from log<sub>10</sub> (*x*+1)-transformed

abundance data to reduce the influence of dominant taxa (Clarke & Warwick 2001). The analysis was performed with 9,999 permutations of residuals under a reduced model and was based on Type II sums of squares, as recommended for unbalanced factorial designs (Langsrud 2003). Owing to low numbers of unique permutations in some cases, statistical significance was assessed using *P*-values obtained via Monte Carlo simulations rather than from permutation-based empirical distributions (Anderson & Robinson 2003). Post hoc permutational *t*-tests were used to resolve pairwise differences among levels of significant terms and the relative contributions of algal taxa to differences between treatments were determined using similarity of percentages analysis (SIMPER; Clarke 1993).

Analyses were conducted in R (version 3.0.1; R Development Core Team 2013), except for distance-based perANOVAs and PERMANOVAs, which were performed using the PERMANOVA+ add-on in PRIMER (version 6.1.13; PRIMER-E Ltd., Plymouth, UK).

## Results

Temporal variability of *Littorina* populations determined the effects of sedimentation on the structure and stability of algal assemblages (Table 2). Macroalgal evenness was reduced by elevated sedimentation when *Littorina* density was constant, but not when *Littorina* densities were variable (perANOVA; consumer variability  $\times$  sedimentation:  $P = 0.035$ ; Table 2a; Fig. 2a). Elevated sedimentation also decreased the number of local extinctions of macroalgal species in both of the variable treatments but not in the constant treatment (consumer variability  $\times$  sedimentation:  $P = 0.015$ ; Table 2b; Fig. 2b). Although consumer variability and sedimentation interacted to affect the spatial variability of both microalgal ( $P = 0.030$ ) and macroalgal ( $P = 0.012$ ) assemblages (Table 2b), post hoc tests were inconclusive and revealed

no significant ( $P < 0.05$ ) differences between ambient and elevated sedimentation for any of the three consumer variability treatments (Fig. 2c,d). A decrease in macroalgal spatial variability in response to elevated sedimentation was, however, bordering on statistical significance in the variable<sub>2</sub> treatment (perANOVA post hoc test;  $t = 2.28$ ,  $P = 0.052$ ).

Independently of sedimentation, increased temporal variability of *Littorina* populations resulted in a shift in macroalgal assemblage structure (PERMANOVA;  $P = 0.012$ ; Table 2a), but this effect depended on the temporal pattern of consumer density fluctuations. Specifically, the ‘variable<sub>2</sub>’ treatment (i.e. commencing with low *Littorina* density), but not the ‘variable<sub>1</sub>’ treatment (i.e. commencing with high *Littorina* density), differed from the ‘constant’ treatment in terms of macroalgal assemblage structure at the end of the experiment (PERMANOVA post hoc test;  $t = 1.66$ ,  $P = 0.024$ ). This difference was driven by greater cover of red (*Osmundea* spp. and *Mastocarpus stellatus*) and green (*Ulothrix* sp.) turf-forming species and encrusting coralline species (‘*Lithothamnium* spp.’) in the variable<sub>2</sub> treatment compared to the other treatments (SIMPER; Table S2).

The nature and temporal pattern of *Littorina* population variability also affected, independent of sedimentation, the compositional turnover of macroalgal assemblages (perANOVA;  $P = 0.010$ ; Table 2b) and their resistance to perturbations in the form of natural environmental fluctuations ( $P = 0.045$ ; Table 2b). Although post hoc tests were unable to resolve differences among groups fully, algal assemblages in the variable<sub>2</sub> treatment appeared to have increased compositional turnover relative to those in the constant treatment (Fig. 2e) and lower resistance to perturbations compared to those in the variable<sub>1</sub> treatment (Fig. 2f).

## Discussion



348

349 Our results demonstrate that **altered patterns of** temporal variability in the population density  
350 of even a single consumer species can, independent of its mean density, affect multiple  
351 aspects of both the structure and stability of natural communities and determine their  
352 responses to **other** perturbations. **Additionally**, we show that the effects of consumer  
353 population variability depend on the timing of density fluctuations, **which, in general,**  
354 **appeared to be more important than variability *per se*.** These findings have important  
355 implications for our understanding of the factors governing ecological responses to  
356 perturbations. In particular, our results indicate that predicting the effects of disturbances on  
357 ecosystems requires knowledge of the patterns of variability in species populations.

358

359 We found that the effects of sedimentation on the structure and stability of algal assemblages  
360 were determined by variability in the densities of *Littorina littorea* populations, independent  
361 of their mean densities. Further, it appeared that the **variability *per se***, rather than temporal  
362 pattern, of consumer **densities** drove this interaction. When consumer densities were held  
363 constant, elevated sedimentation resulted in a decline in macroalgal evenness, which can be  
364 explained by a reduction in the recruitment and/or survival of less tolerant species and a  
365 subsequent shift in dominance towards more resistant species (Airolidi 2003). **Mechanisms by**  
366 **which sediment can affect algal species directly include damage to or loss of individuals via**  
367 **scouring and abrasion, reduced availability of stable substratum as a result of sediment build-**  
368 **up, and restricted access to light, oxygen and nutrients owing to burial and smothering**  
369 **(Airolidi 2003).** Although sedimentation can directly impair the feeding activity of gastropod  
370 grazers such as limpets (Airolidi & Hawkins 2007), it may have weaker effects on more  
371 mobile species, particularly at greater densities. In fact, *L. littorea* has been shown to  
372 ‘bulldoze’ accumulated sediment from rocky substrata, indirectly inhibiting the development

of algal canopies (Bertness 1984) and mitigating the negative effects of sedimentation on more susceptible ephemeral algal species (Airolidi 2003). It is therefore possible that the effects of elevated sedimentation on the growth of certain algal species were negated by periods of higher grazing pressure within the variable treatments, with consequences for algal evenness. Consistent with this, elevated sedimentation reduced the number of local extinctions of macroalgal species when *L. littorea* densities were variable, with a tendency towards homogenising algal cover in space. In our study, which was conducted on open emergent substrata on a moderately exposed rocky shore, there appeared to be little opportunity for the extensive accumulation of sediment within experimental plots (pers. obs.). Further, although we did not characterise background sedimentation rates, our elevated sedimentation treatment involved the addition of quantities of sediment that were relatively small in the context of natural sedimentation regimes on other temperate rocky shores (Airolidi & Virgilio 1998; Connell 2005). Despite the observed responses of algal assemblages to this treatment, these factors may have limited the effect of sedimentation on our other measures of structure and stability. Overall, however, our results demonstrate that the ecological effects of such perturbations can depend strongly on the nature of temporal variability in biotic communities.

Independent of sedimentation, increased consumer variability resulted in a shift in macroalgal assemblage structure relative to when consumer density was held constant. Similar results have been found previously in aquatic systems where resource species differed in their growth rates and susceptibility to predation and consumers exhibited prey selectivity (Butler 1989; Navarrete 1996). However, this shift observed in our experiment occurred only in the ‘variable’ treatment commencing with a high consumer density (variable<sub>2</sub>), and not in the treatment commencing with a low density (variable<sub>1</sub>). The timing of disturbance events has

been shown to have important consequences for the emergent structure of recovering communities when species differ in terms of reproductive and phenological traits, in addition to their relative susceptibilities at different life history stages (Hawkins 1981; Airolidi 2000). It is possible that differences in consumer densities between variability treatments at the start of the experiment influenced the relative rates of establishment among algal species, resulting in divergent successional trajectories that contributed to the observed differences in final assemblage structure. Additionally, the temporal coincidence between maximum grazer densities and periods of peak recruitment of algal species throughout the duration of the experiment may have contributed to the observed shifts in algal assemblage structure (Bertocci *et al.* 2005). For example, in the variable<sub>2</sub> treatment, peaks in grazing corresponded with the main reproductive periods of *Fucus vesiculosus*, i.e. September–October and May–June (Berger *et al.* 2003). The final macroalgal assemblage structure in this treatment was characterised by a relatively low abundance of this species. Similarly, differences in the abundances of some algal species, particularly fast-growing ephemeral species, may be a function of grazer density immediately prior to the final census date. For example, the abundances of *Porphyra umbilicalis* and *Ulva lactuca*, which are preferred food items for *L. littorea* (Lubchenco 1978), were greater in the variable<sub>2</sub> treatment compared to the constant and variable<sub>1</sub> treatments. However, if patterns in final assemblage structure were based predominantly on direct consumptive effects of grazing, we would expect differences to be driven by such palatable ephemeral species. In contrast to this expectation, unpalatable perennial species, such as *Osmundea* spp. and *Mastocarpus stellatus*, made a far greater contribution to differences in assemblage structure between these treatments. This suggests strongly that other indirect processes, such as competitive interactions among species, were important in mediating the responses of algal communities to temporal patterns of grazing (Airolidi & Cinelli 1997).

423

424 Both the compositional turnover and the extent of structural change (resistance) of algal  
425 assemblages in response to environmental fluctuations depended on the temporal pattern of  
426 consumer density fluctuations. There was, however, no consistent effect on overall  
427 community stability of any particular treatment. Specifically, resistance to environmental  
428 fluctuations appeared to be greatest in the variable<sub>1</sub> treatment and lowest in the variable<sub>2</sub>  
429 treatment, whereas compositional turnover was greatest in the variable<sub>2</sub> treatment and lowest  
430 in the constant treatment. Although the underlying mechanisms are unclear, such effects may  
431 occur indirectly via changes in the relative abundances of key species that modify competitive  
432 interactions within the community and, therefore, contribute to multiple components of  
433 stability. For example, in temperate grassland ecosystems, the existence of competitive  
434 hierarchies involving dominant ‘core’ species that interact with less abundant ‘satellite’  
435 species may promote biotic feedback instabilities, leading to the destabilisation (i.e. increase  
436 in variability) of communities (Collins 2000). Similar processes may operate within intertidal  
437 macroalgal assemblages, which are also characterised by competitive asymmetries at multiple  
438 life stages (Berger *et al.* 2003; Maggi *et al.* 2012). Additionally, certain species may modify  
439 the influence of exogenous environmental variability on communities in different ways, with  
440 contrasting consequences for stability. In marine intertidal systems, for example, habitat  
441 engineers such as mussels may enhance the transmission of environmental stochasticity  
442 through communities, increasing the temporal variability of other species (Wootton 2010).  
443 Conversely, on some rocky shores, canopy-forming algae may dampen oscillations in  
444 physical conditions and promote asynchronous species fluctuations, resulting in decreased  
445 overall community variability (Bulleri *et al.* 2012). Thus, changes in both biotic and  
446 environmental feedback pathways resulting from the shift in balance away from structurally  
447 important forms of perennial algae (*Mastocarpus stellatus* and *Fucus vesiculosus*), as

observed in the variable<sub>2</sub> treatment, may have contributed to the destabilisation of assemblages in this treatment. In general, the mechanisms by which population variability affects the stability of complex communities require further investigation, paying particular attention to the relative contribution of particular species to different components of stability (Ives & Carpenter 2007). Importantly, while previous studies have shown that species loss can have dramatic effects on assemblage structure and stability (O’Gorman & Emmerson 2009; Donohue *et al.* 2013), we have shown that more subtle biotic perturbations, such as changes in the temporal variability of a single key species, may also affect multiple aspects of ecosystem functioning and stability.

In a mesocosm experiment, Atalah *et al.* (2007) found that increased temporal variability of grazing resulted in reduced total algal cover. In contrast to this, however, we found no effect of consumer variability on either microalgal biomass or macroalgal cover in our field experiment. Further, the temporal variability of both microalgal and macroalgal cover was also unaffected by alterations to grazing variability. These results suggest that the biomass and temporal variability of communities in our study were regulated more strongly by processes other than variability in grazing intensity. This may be because environmental heterogeneity in the field masked the effects of consumer population fluctuations on total algal abundance and variability. Additionally, within diverse algal assemblages, strong competitive interactions among species can result in compensatory responses (Maggi *et al.* 2012) whereby opposing changes in individual species abundances may underlie constant total algal abundance. Indeed, we observed a shift in macroalgal assemblage structure resulting from changes in the abundances of individual algal taxa, which were perhaps mediated by interactions between species.

We designed our consumer variability treatments in the absence of detailed information about natural fluctuations of *Littorina littorea* populations at the study site. During the course of our experiment, however, our uncaged unmanipulated plots revealed background patterns of population variability (Fig. 1a). While the mean density and magnitude of fluctuations of *L. littorea* populations were both similar between uncaged and caged plots, the frequency of fluctuations in our experimental manipulations was slightly greater than that observed on the shore. However, differences in the responses of algal assemblages between uncaged and caged plots may have been a result of artefacts from the use of cages, in concert with differences between natural and manipulated patterns of consumer variability. The lack of true procedural controls in our experiment, necessitated by difficulties in manipulating consumer densities without the use of cages, limits how far we can extend our inferences to natural communities. Despite this, examining differences among our caged treatments enabled us to test the effects of consumer variability and sedimentation on natural multitrophic assemblages exposed to realistic levels of natural environmental heterogeneity and open to propagule supply. Within a given area, temporal variability in natural populations may occur both as a result of community processes, including consumer–resource dynamics, and in response to environmental heterogeneity, such as seasonal changes in conditions (Butler 1989; Navarrete 1996; Lauzon-Guay & Scheibling 2009). Owing to the potential for complex interactions between intrinsic and extrinsic drivers of population variability, and their additional effects on ecosystem functioning and stability, it is difficult to disentangle the ecological role of population variability itself from other such influences in natural systems. Consequently, community responses to changes in natural versus manipulated patterns of consumer variability may differ. Thus, while our results demonstrate the importance of consumer variability when manipulated in isolation, enhancing the applicability of these findings to natural stochastic systems requires greater understanding of the modifying roles of

community dynamics and environmental variability. Another caveat of our study is that it does not account for the potential role that population density plays in mediating the effects of temporal variability. Although we separated the effects of variability and temporal pattern from that of mean density, logistical constraints prevented us from testing for an interaction between these variables (Benedetti-Cecchi *et al.* 2005). Further experimentation, involving a range of grazer density treatments, would help to clarify the relative contribution of density to the observed effects of consumer variability on community stability.

In conclusion, our study demonstrates that altered patterns of temporal variability within the population of a single species may propagate through food webs to influence multiple aspects of the structure, functioning and stability of communities. Importantly, we found that the effects of such disturbances cannot be predicted without knowledge of the temporal pattern of density fluctuations. Moreover, to our knowledge, this study is the first to show that alterations to the temporal variability of single populations can determine how communities respond to other perturbations. Overall, our findings indicate that the ecological impacts of disturbances, which may be unpredictable because of interactions among different temporal patterns of perturbations (García Molinos & Donohue 2010) as well as different types of stressors (Crain, Kroeker & Halpern 2008), are mediated by patterns of temporal variability within communities. Therefore, the consequences of disturbances are likely to be highly context-dependent with respect to the timing of environmental fluctuations and temporal coincidence of disturbance events (see also Pincebourde *et al.* 2012). Our work also emphasises the value of a multidimensional view of ecological stability in facilitating a more complete understanding of community responses to perturbations (Donohue *et al.* 2013). To improve our predictions of the ecological impacts of perturbations in a changing world, we

require greater appreciation of the importance of temporal patterns of variability and, in particular, the reciprocal relationship between community structure and stability.

## **Acknowledgements**

We thank S.J. Hawkins, J.D.R. Houghton and one anonymous reviewer for useful comments on an earlier draft of this manuscript. We are also grateful to E. Nolan, B. Tamland and L. Taplin for providing assistance in the field. This study was completed as part of a PhD studentship funded by the Department for Employment and Learning Northern Ireland.

## **Data accessibility**

Species abundance data are available via the Dryad Digital Repository (doi: xx.xxxx/dryad.xxxx).



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#### **Supporting Information**

Additional supporting information may be found in the online version of this article:

**Table S1.** Results of tests for differences in macroalgal assemblages among treatment combinations at the start of the experiment.

**Table S2.** Relative contributions of macroalgal taxa to differences in assemblage structure between consumer variability treatments.

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## Tables

**Table 1.** Components of ecological stability quantified in this study and their measurement (see Pimm 1984 and Donohue *et al.* 2013).

Stability component	Description and quantification
Spatial variability	The coefficient of variance (CV) of total algal abundance (microalgal biomass or macroalgal cover) among experimental plots within each treatment combination on each census.
Temporal variability	The CV of total algal abundance (microalgal biomass or macroalgal cover) in each experimental plot over time.
Number of extinctions <sup>†</sup>	Also known as <i>structural robustness</i> . Calculated as the number of macroalgal taxa that were recorded on the first census date in each plot, but which were absent at the end of the experiment.
Number of invasions <sup>†</sup>	A measure of community <i>persistence</i> . The number of macroalgal taxa that were recorded at the end of the experiment in each plot, but which were absent on the first census date.
Compositional turnover <sup>†</sup>	The extent of change in community composition over time, integrating aspects of temporal variability, resistance, extinctions and invasions. Calculated as the mean Jaccard similarity in macroalgal community composition (based on taxonomic presence/absence data) between consecutive sampling dates for each plot.
Resistance <sup>†</sup>	Calculated as the reciprocal of the Euclidean distance from each experimental plot to the centroid of the uncaged unmanipulated plots at the end of the experiment, based on Bray-Curtis dissimilarity matrices calculated from $\log_{10}(x+1)$ -transformed algal abundance data. Thus, this measure represents the extent of structural change in communities in different experimental treatments in response to natural environmental fluctuations.

<sup>†</sup>Quantified for macroalgal assemblages only.

**Table 2.** Results of PerANOVAs and PERMANOVA testing the effects of consumer variability (constant, variable<sub>1</sub> and variable<sub>2</sub>) and sedimentation on (a) measures of abundance, diversity and structure and (b) components of ecological stability of microalgal and macroalgal assemblages. For univariate analyses involving unbalanced datasets, 95% CIs are based on *F*-values from conventional ANOVAs performed on 10<sup>4</sup> balanced datasets (*n* = 4) sampled randomly from the full dataset. Significant *P*-values are highlighted in bold.

Variable	Source of variation	df	MS	Pseudo- <i>F</i> (95% CI)	<i>P</i>
(a) Abundance, diversity and structure					
Microalgal biomass	Consumer variability, V	2	0.37	2.81 (0.77, 6.78)	0.077
	Sedimentation, S	1	0.06	0.43 ( $8 \times 10^{-4}$ , 2.98)	0.514
	V $\times$ S	2	0.14	1.02 (0.19, 5.00)	0.376
	Residual	34	0.13		
Macroalgae:					
Total cover	V	2	42.09	1.24 (0.12, 4.11)	0.302
	S	1	0.08	$2 \times 10^{-3}$ ( $3 \times 10^{-4}$ , 2.13)	0.962
	V $\times$ S	2	4.51	0.13 (0.02, 1.96)	0.877
	Residual	34	33.99		
Species richness	V	2	0.14	0.08 (0.02, 1.49)	0.925
	S	1	0.63	0.34 (0.06, 2.36)	0.561
	V $\times$ S	2	5.72	3.16 (0.16, 5.24)	0.057
	Residual	34	1.81		
Species evenness	V	2	$2 \times 10^{-3}$	0.20 ( $5 \times 10^{-3}$ , 0.84)	0.811
	S	1	$2 \times 10^{-3}$	0.26 ( $1 \times 10^{-4}$ , 0.69)	0.613
	V $\times$ S	2	0.03	3.71 (0.68, 3.13)	<b>0.035</b>
	Residual	34	0.01		
Assemblage structure	V	2	2381.80	2.28 -	<b>0.012</b>
	S	1	791.17	0.76 -	0.608
	V $\times$ S	2	1079.10	1.03 -	0.420
	Residual	34	1044.40		
(b) Stability components					
Microalgae:					
Spatial variability	Month, M	7	40.11	17.84 -	<b>&lt;0.001</b>
	V	2	6.91	3.08 -	0.060
	S	1	2.98	1.32 -	0.255
	V $\times$ S	2	8.72	3.88 -	<b>0.029</b>
	Residual	35	2.25		
Temporal variability	V	2	0.04	0.37 (0.01, 1.97)	0.696
	S	1	0.05	0.52 ( $4 \times 10^{-4}$ , 1.53)	0.479
	V $\times$ S	2	0.10	0.96 (0.22, 2.34)	0.396
	Residual	34	0.10		

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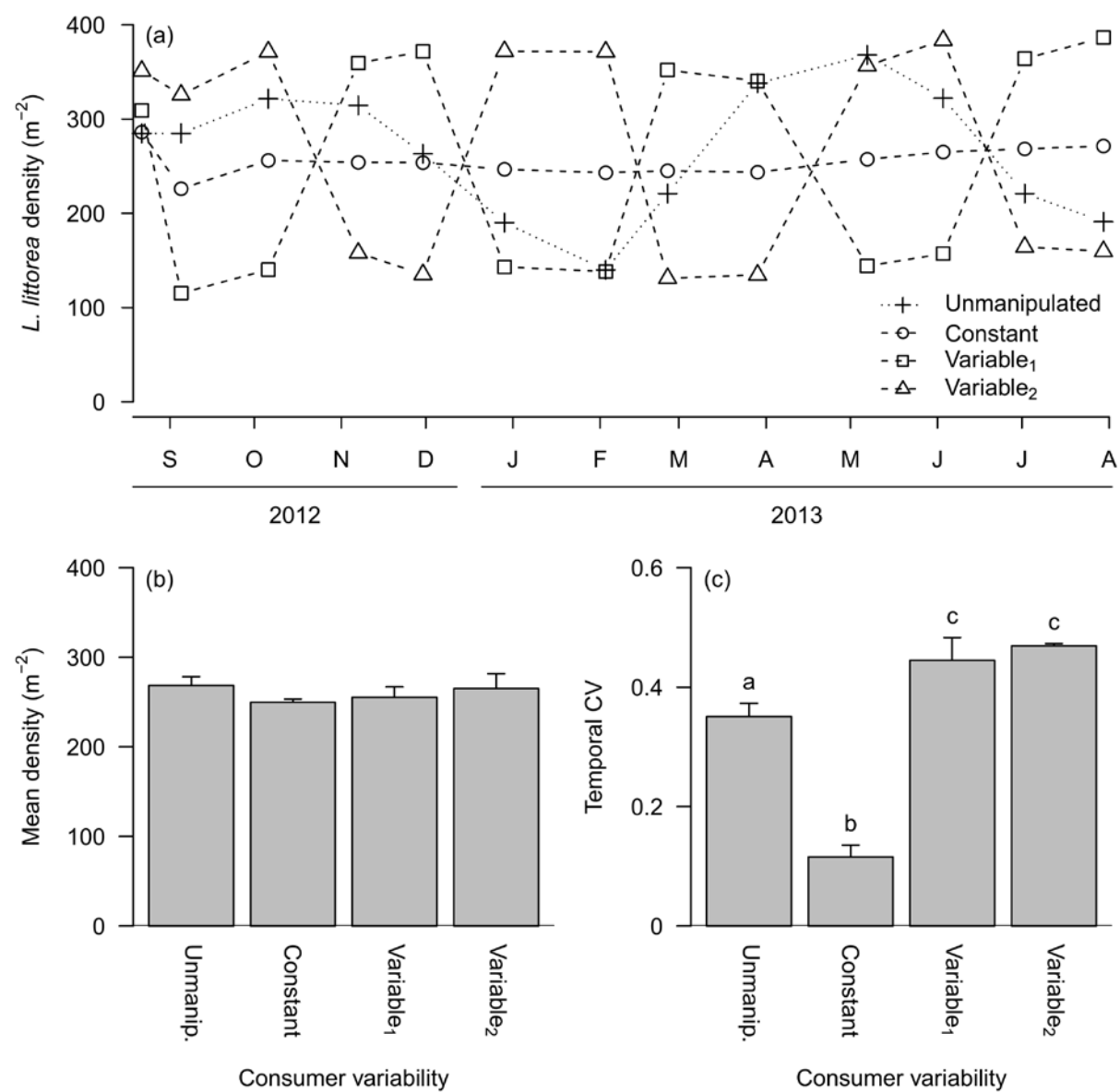
(Table 2 continued)

Macroalgae:						
Spatial variability	M	8	0.04	1.70	-	0.132
	V	2	0.15	7.16	-	<b>0.002</b>
	S	1	0.03	1.53	-	0.223
	V × S	2	0.11	4.91	-	<b>0.014</b>
	Residual	40	0.02			
Temporal variability	V	2	0.01	2.42	(0.69, 7.54)	0.103
	S	1	$4 \times 10^{-3}$	0.66	( $6 \times 10^{-3}$ , 4.04)	0.415
	V × S	2	0.01	1.88	(0.33, 5.22)	0.168
	Residual	34	0.01			
No. of extinctions	V	2	3.97	7.88	(3.29, 10.32)	<b>0.002</b>
	S	1	3.60	7.15	(2.35, 14.49)	<b>0.012</b>
	V × S	2	2.42	4.80	(1.63, 5.64)	<b>0.017</b>
	Residual	34	0.50			
No. of invasions	V	2	4.27	2.76	(0.83, 6.27)	0.084
	S	1	4.90	3.17	(0.10, 8.35)	0.085
	V × S	2	0.77	0.50	(0.03, 2.68)	0.608
	Residual	34	1.55			
Resistance	V	2	0.32	3.39	(2.06, 5.70)	<b>0.045</b>
	S	1	0.01	0.12	( $9 \times 10^{-4}$ , 7.21)	0.746
	V × S	2	0.15	1.60	(0.46, 4.59)	0.214
	Residual	34	0.09			
Compositional turnover	V	2	0.02	5.15	(2.36, 8.59)	<b>0.010</b>
	S	1	0.01	1.21	(0.08, 8.99)	0.278
	V × S	2	0.01	2.38	(0.82, 6.45)	0.111
	Residual	34	$4 \times 10^{-3}$			

## Figure legends

**Fig. 1.** (a) Monthly mean densities, (b) overall mean (+ 1 SE) densities and (c) temporal variability (detrended coefficient of variation; mean + 1 SE) in the density of *Littorina littorea* over the duration of the experiment in uncaged unmanipulated plots ( $n = 8$ ) and in caged plots belonging to consumer variability treatments (constant and variable<sub>1</sub>,  $n = 8$ ; variable<sub>2</sub>,  $n = 4$ ). In (c), different letters denote groups of treatments that are significantly different from each other ( $P < 0.05$ ) based on SNK tests.

**Fig. 2.** Mean (+ 1 SE) (a) Simpson's evenness ( $1-\lambda$ ) of macroalgal assemblages, (b) number of local extinctions of macroalgal species, spatial variability of (c) micro- and (d) macroalgal assemblages, (e) compositional turnover of macroalgal assemblages and (f) resistance of macroalgal assemblages to natural environmental fluctuations over the duration of the experiment in uncaged unmanipulated plots ( $n = 8$ ) and in caged plots belonging to consumer variability treatments (constant and variable<sub>1</sub>,  $n = 8$ ; variable<sub>2</sub>,  $n = 4$ ). Results from uncaged plots were not included in statistical analyses but are included here to provide additional context. Asterisks indicate significant differences between groups (\*\* $P < 0.05$ ) based on perANOVA post hoc tests. Different letters denote groups of treatments that are significantly different from each other ( $P < 0.05$ ) based on SNK tests.



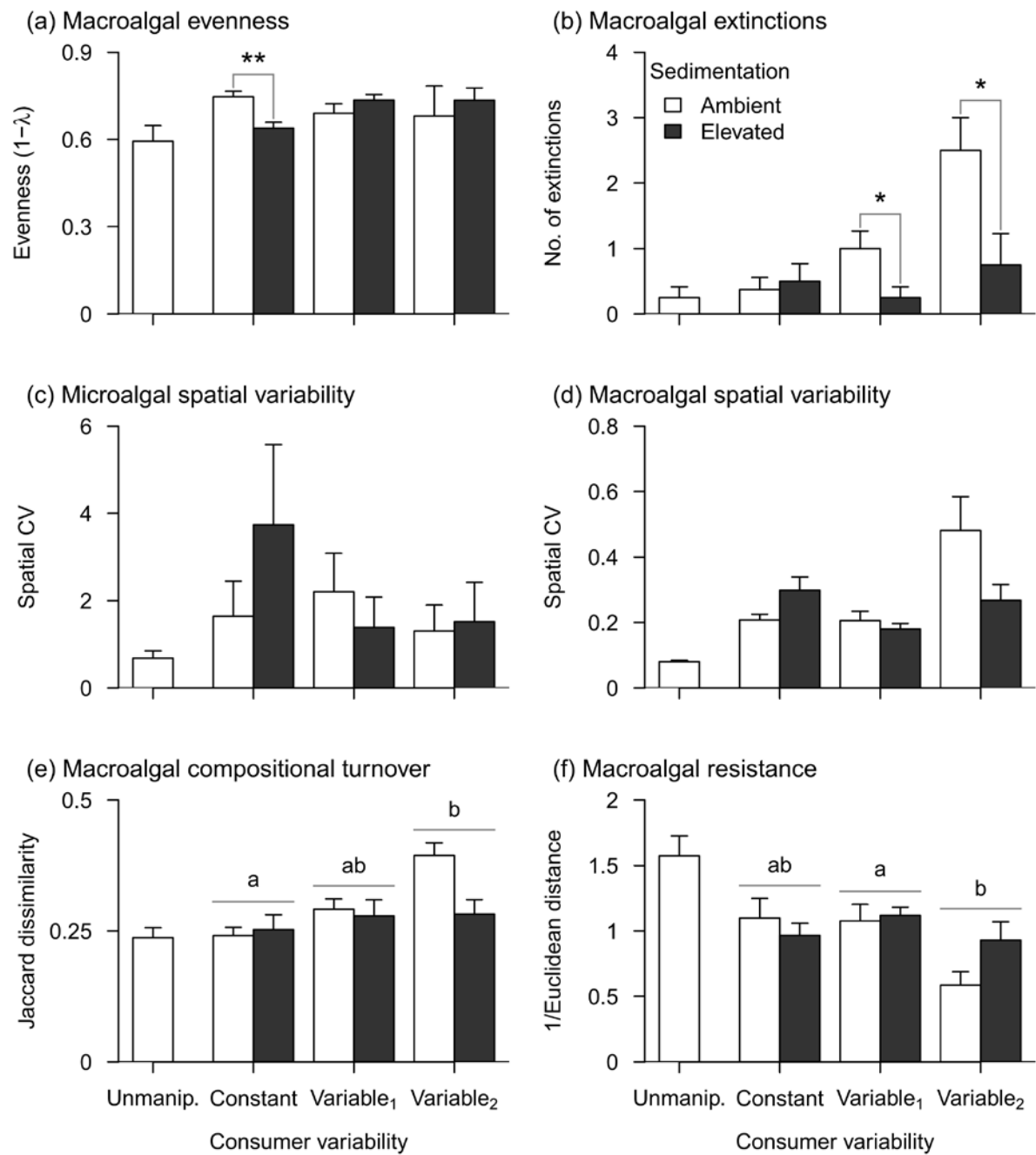
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**Fig. 2.** Mrowicki *et al.*